THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[THIRD SERIES.]

"...... per litora spargite muscum, Naiades, et circum vitreos considite fontes ; Pollice virgineo teneros he carpite flores ; Floribus et pictum, divæ, replete canistrum. At vos, o Nymphæ Craterides, ite sub undas ; Ite, recurvato variata coralia trunco Vellite muscosis e rupibus, et mihi conchas Ferte, Deæ pelagi, et pingui conchylia succo." N. Parthenii Giannettasii Ecl.1.

No. 109. JANUARY 1867.

I.—On the Organs of Circulation of the Roman Snail (Helix pomatia). By CHARLES ROBERTSON, Demonstrator and Curator of the Anatomical Collection, Oxford.

[Plate I.]

THE very imperfect account given in most of the standard works on comparative anatomy of the organs of circulation of the Gasteropoda has induced me, from time to time, to try various experiments and injections for the purpose of determining the course of the blood and the existence of a capillary system between the arteries and veins*.

The majority of recent writers agree in their accounts of the vascular system, and describe the artery and its branches as far as the head, where it is said to terminate in a sinus which surrounds the nerve-collar, and this, again, communicates with other sinuses in other parts of the body. These spaces left between the artery and vein have been named lacunæ, or intervisceral spaces; and the circulation is therefore said not to be closed throughout its course, and the capillary system is generally wanting.

Milne-Edwards, in his elaborate and instructive paper on the organs of circulation of the Mollusca, describes the arterial and

* Owen's Lectures on Comparative Anatomy (1855), p. 559; Carpenter's Comparative Anatomy (1854), p. 252; Siebold, Anatomy of the Invertebrata, translated by W. L. Burnett (1854).

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venous systems of the Snail, and the lacunæ which form the means of communication between them; but the exact course which the blood takes on its way back to the pulmonary chamber is not very definitely pointed out, or any description given of the capillary system*.

In the present paper I propose giving the result of a numerous series of observations and injections of the Roman Snail (Helix pomatia); but, before proceeding to give a detailed description of the vascular system, I will describe the method adopted for killing the animals, and the substances used for injecting them. When the animals are killed with chloroform, spirits of wine, or warm water, the foot of the animal is generally so much contracted and rigid, that it is quite impossible to get the injection to run far without much of it extravasating amongst the viscera. After many trials with the above and various other substances, I at last found the following method of killing them answer remarkably well :-- Place the animal in a jar of cold water, and exclude all air by placing a glass cover over the top, and allow it to remain undisturbed till it is drowned, when the foot will be found as fully distended and as soft and flexible as when the animal is living. It generally takes forty-eight hours to kill them in this way. Of injections, I have found that size mixed with various colouring matters has answered better than cold coloured fluids. The size, when injected very gently into the vessels, clings to them, and gives a certain amount of support to their delicate walls. I have found the finest gelatine and carmine run exceedingly well, and it has made some very beautiful preparations. Cold injections have this disadvantage, that, on account of the soft and flexible nature of the parts, it is necessary to keep the animal in water during injection, and also when it is dissected. With fluid injections, the least pressure with the hand, or in lifting the animal from one dish to another, may cause the fluid to escape from the vessels, or shift its position; and thus false results are obtained. When size is used, and the animal is not shifted during injection or, better, till the injection has set, you have an exact mould of the vessels, which does not shift its position during dissection.

Milne-Edwards, in his experiments on the snail[†], used chromate of lead and size, and the injection-pipe was passed into a hole made by an instrument in the base of the tentacle. Injections made in this way fill first the lacunæ or spaces between the viscera, and finally reach the pulmonary chamber. I have tried many injections in this way, and also by thrusting the injectionpipe into the substance of the foot; but I have always considered it a very unsatisfactory method of proceeding; and although it

* Ann. des Sciences Nat. sér. 3. tome iii. p. 295. † Ibid. p. 294.

is quite possible to inject parts of the animal in this way, it is done on the supposition that lacunæ exist in the body, and that the injection will find its way from them into the vessels. I have therefore tried injections from the aorta, the venous sinus, and pulmonary vein, as well as the foot.

Before I proceed to give a detailed account of the vascular system, I will give in detail the results obtained from injections both from the tentacle and the aorta, selected from a large number of experiments.

Animal killed in a jar of cold water; the the foot and tentacle extended, but not much swollen with the water. Injected from the tentacle with warm size and carmine. After cooling, the foot and skin were uniformly red, and no appearance of extravasation on their surfaces. On opening the body, the injection was found to have returned to the heart by the pulmonary vein, injecting the anterior part of the pulmonary chamber, but neither the kidney nor that part of the pulmonary chamber situated between it and the rectum. None of the injection had found its way into the aorta or its branches. The surface of the crop and the salivary glands were well injected. A large mass of injection moulded between the viscera fell out easily when touched with the end of a scalpel. The venous sinus which runs along the side of the rectum filled well, and also the capillaries on the surface of the oviduct and vas deferens.

Animal killed in the same way as the last. The parts presented much the same appearance. Injected from the ventricle with size and carmine. On opening the body after cooling, the injection was found to have gone right round the body and returned to the pulmonary chamber, richly injecting the space of the pulmonary sac between the rectum and kidney (Pl. I. fig. 2d). A small quantity of injection was found in the pulmonary vein (fig. 2b). In this case, and in some other snails injected in the same way, I observed on the surface of the multifid vesicles and in other parts of the body small masses of carmine moulded between the cæca. When detached and placed in warm water, the whole dissolves, without leaving any trace of enveloping membrane: I consider these masses of carmine are merely masses of extravasation from the delicate walls of the capillaries. The capillaries of the digestive tract and generative organ most beautifully injected. The surface of the skin and foot uniformly red. Only a small quantity of extravasation found round the collar, and none observed in other parts of the body.

I might give numerous other examples, selected from my notes; but the results are generally the same, and the two examples I have selected give fairly the results of both methods of investigating such delicate structures. Of course it is difficult

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to make a perfect injection of such delicate animals without some extravasation. If these two examples are placed side by side, and a comparison made of the vascular system, it is quite obvious that in the first example the injection had only filled the venous system, and left the arterial quite empty. Injection performed in this way fills first large spaces in the body, then the venous capillaries of the viscera, and lastly the pulmonary capillaries, before it reaches the heart; and a good deal of pressure is required to get it thus far. In the second experiment the injection was thrown into the natural starting-point of the circulatory current; and, for the present, I attach great importance to the fact of the whole vascular system being well filled, and only a small quantity of extravasation being found, round the nerve-collar,—most likely the result of a little too much pressure on the syringe.

The heart of the snail consists of a single auricle and ventricle enclosed in a pericardium (Pl. I. fig. 2a), which is situated at the posterior and left extremity of the pulmonary chamber, about the middle of the lower border of the kidney (fig. 2e). The delicate auricle receives the blood by a large pulmonary vein (fig. 2 b) from the surface of the pulmonary sac and kidney, and propels it into the ventricle, which is situated behind it and on the same plane. The aorta (fig. 1 j), after leaving the ventricle, perforates the peritoneal covering of the viscera, and passes into the abdominal cavity between a loop of intestine and the anterior margin of the liver, with the receptaculum seminis closely adhering to its right surface. It soon gives off two trunks (fig. 1 k) for the posterior part of the crop, the liver, and the whole of the viscera placed in the spire of the shell. The first of these trunks is the largest, and gives twigs to that part of the digestive tract contained in the spire of the shell. The second of these branches is much smaller, and is lost on the posterior portion of the crop and the albuminiparous gland and that part of the intestine which runs along the side of the pulmonary chamber. The aorta, after giving off these branches, bends forwards, having the crop on its inferior surface and the conjoined generative ducts above it. The next trunk which proceeds from it is a stout branch, and is given off when the aorta in its forward course reaches the posterior and right extremity of the salivary gland. This trunk again breaks up into three branches, which all spring from the same point. The first branch (fig. 1 l) passes to the right and supplies the sides of the body, and then passes down and is lost in the upper portion of the foot. The second branch runs to the left (fig. 1 n), and is lost on the surface of the crop and salivary glands. The third branch (fig. 1m) passes straight down between the retractor muscles of the head,

and supplies the posterior portion of the foot with blood. The aorta, after giving off these trunks, runs straight forward to the inferior α sophageal ganglion (fig. 1 p) without giving off any large branches, having the crop on its superior surface, the retractor muscle of the head below, with the visceral nerve closely adhering to its left side. After perforating the inferior esophageal ganglion, it splits into two branches, the first and smaller of which proceeds into the buccal mass. A small branch comes up on each side of the infra-œsophageal mass, adhering closely to the nerve-collar, supplies the tentacles (fig. 1 o), parts about the head, the whip and sheath of the penis, and anterior sides of the body. The second and larger bends sharply back round the inferior surface of the ganglion, and runs along the surface of the foot between the bundles of retractor muscles (fig. 1q), and gives off branches throughout its course to all those parts not supplied by the posterior pedal*. The aorta therefore does not, as Milne-Edwards and others maintain, when it reaches the head, terminate in a large sinus which surrounds the collar, but can with ease be traced into the substance of the foot, where it ends in a capillary system.

Two large veins collect the venous blood from the capillaries of the body, foot, &c., and unite to form a large sinus, which runs along the side of the rectum; and from it the blood passes to the pulmonary capillaries. The most superficial of these veins commences at the posterior part of that portion of the liver which is contained in the spire of the shell, runs along the thickened rim of the mantle, receives in its course numerous large twigs which come up from the surface of the liver, and forms a junction with the second vein at the posterior extremity of the pulmonary chamber. The second vein collects the blood from the foot, the mantle, the skin covering the head, the anterior and lower surface of the liver, and forms a considerable sinus, which runs along the posterior border of the kidney and finally joins the first superior vein, to form a sinus at the point where the rectum leaves the visceral covering. A third and much smaller trunk runs along the wall of the intestine, receiving the blood from its rich plexus of capillaries, and, getting larger as it proceeds towards the rectum, enters the venous sinus close by the last two veins. The large sinus formed by the junction of these three veins runs along the outer border of the rectum (fig. 2 c), covered over by the mantle which is common to both, and when it reaches the pulmonary orifice it closes over its inferior surface and runs across in the thickened border of the mantle, giving off twigs to the whole of the pulmonary chamber.

* For Cuvier's brief account of the vascular system of *Helix*, see 'Mémoires des Mollusques,' Paris, 1817; or Ann. du Muséum, 1806, p. 159.

Injections show that the whole of the venous blood is returned to the sinus by the three veins I have described before it is distributed to the pulmonary capillaries; none of it returns along the anterior border of the mantle and so into the capillaries. If a transverse section is made of the intestine, venous sinus, and duct of the kidney, about the middle of their course (fig. 2 c), they will be found arranged in the following manner. The intestine has the venous sinus on its outer border, and the duct of the kidney on its inner; the duct of the kidney is much stouter than the sinus, but both have about the same calibre.

There is not much difficulty in making a successful injection of the venous system from the sinus, by the side of the rectum, the injection spreading very readily from the veins into the capillaries, and, if not too much pressure is used, without extravasating amongst the viscera^{*}.

As I have before observed, the capillaries may be injected from the aorta, or by thrusting a pipe into the tentacle, or from the venous sinus. Injection performed in either of these ways fills a rich plexus of vessels on the whole of the digestive tract, the generative organs, mantle, and foot, before presenting any trace of lacunæ amongst any of these organs. I have repeatedly injected from the aorta, and have found the capillaries richly injected, as well as the venous system, without any trace of lacunæ or intervisceral spaces being observed between the arteries and veins. I have therefore come to the conclusion that the vascular system is closed in Helix pomatia, and that the arteries and veins are connected by a capillary system, and the blood is not shed into lacunæ in any part of the body. If the injection of these delicate animals is not very carefully performed, and the body quite soft and flexible before the injection is thrown in, it will very readily form large masses amongst the viscera. If one of these masses from a warm injection is carefully picked out, and placed in warm water, the whole of the injection readily dissolves, and does not leave any trace of enveloping membrane, which, I think, shows conclusively that if lacunæ do exist in the body, they are not dilatations of the venous system, but must be spaces excavated in the body without any independent walls. I have repeatedly examined the whole of the abdominal cavity, for the purpose of making out any communication between it and the venous system, without finding any. If the veins have any direct communication with the cavity of the body, and a size

* The vessels of *Helix algira* are figured by Carus and Ottone, part 6. tab. 2. fig. 5, from Erdl's 'Dissert. inauguralis de *Helicis algira* vasis sanguiferis, 1840,' which I have not seen. Siebold considers that they are arteries which are figured (Anatomy of the Invertebrata, p. 248); but I am quite confident that they are veins which are figured, and that Erdl is right. injection is thrown in and allowed to cool, some trace of these communications ought to be found.

If my experiments are correct, the course of the blood after leaving the heart will be as follows :-- From the artery it passes into a plexus of capillaries, which are richly spread over the whole of the body, and from them it is collected into veins with distinct walls, which return the whole of it to a large sinus by the side of the rectum (Pl. I. fig. 2 c). From this sinus the blood passes, first, into the capillaries of the pulmonary sac, which is situated between the rectum and kidney (fig. 2d), and, lastly, runs forward and round into the whole of the anterior portion of the sac, the whole of the venous blood being thus aërated before returning to the heart. The arterial blood which is collected from the posterior narrow slip of pulmonary sac passes through the kidney (fig. 2e) before it reaches the pulmonary vein. The kidney, therefore, is supplied with blood which has been previously aërated in the pulmonary capillaries; but the whole of the venous blood does not pass through it*.

I think it extremely probable that, with improved injectionfluids and injecting-apparatus, and by paying attention to the state of the animal before the injection is begun, a closed system of vessels will be found in other Gasteropoda. Messrs. Hancock and Embleton, after describing the arterial and venous systems of the Eolis, and the mode of communication between these systems, go on to remark+, "We cannot undertake to say whether they end by closed extremities, or whether they have open mouths which communicate with lacunæ or sinuses in the intervisceral spaces, or with those in the skin. The lacunæ in the viscera we have not been able to make out by dissection, and have not made use of injections on account of the great difficulty of injecting such small animals." Also, in their account of the vascular system of the Nudibranchiate Mollusca[‡], "The parietal or hepatic system is probably provided with a complete system of capillaries."

EXPLANATION OF PLATE I.

The arterial system of *Helix pomatia*, from a photograph by Messrs. Wheeler & Day, Oxford.

Fig. 1. The foot has been placed downwards, and the dissection made

1 Alder and Hancock's 'Nudibranchiate Mollusca,' vii. p. 15.

^{*} Milne-Edwards says that the whole of the venous blood is not obliged to traverse the pulmonary chamber before reaching the heart, part of it being carried by a system of canals and vessels to the kidney (Lecons sur la Physiologie et l'Anatomie Comparée, vol. iii. p. 148). Prof. Lawson says that a capillary system does not exist in *Limax maximus* (Quart. Journ. Microscopical Science, January 1863).

[†] Anatomy of Eolis, Ann. Nat. Hist. (1848), vol. i. p. 100.

from above; the pulmonary chamber has been turned to the left and the generative organs to the right. a, foot; b, pulmonary vessels; c, spire; d, rectum; e, kidney; f, albuminiparous gland; g, anterior pedal artery; h, multifid vesicles; i, penis; j, aorta just where it perforates the peritoneal covering of the viscera (the pericardium has not been laid open, so the heart is not seen); k, branch to stomach and contents of spire; l, branch to the side of the body; m, branch to posterior portion of the foot; n, branch to salivary glands and crop; o, branch to tentacles, penis, and parts about the head; p, point where the aorta perforates the infra-œsophageal mass and bends back to enter the foot (part of the ganglion has been cut away); q, branch to generative ducts.

- Fig. 2. The pulmonary chamber, heart, kidney, and venous sinus of the same: a, heart; b, pulmonary vein; c, venous sinus; d, narrow portion of pulmonary chamber between the rectum and kidney; e, kidney, which has been laid open; its duct runs along the inner surface of the rectum, and terminates close by the pulmonary orifice; f, rectum.
- II.—On Pauropus, a New Type of Centipede. By Sir JOHN LUBBOCK, Bart., V.P. Linn. Soc., Pres. Ent. Soc., V.P. Ethn. Soc., F.R.S., &c.*

THE subject of the following communication is a small, white, bustling, intelligent, little creature, about $\frac{1}{25}$ of an inch in length, and may be characterized as follows :—

Body composed of ten segments, including the head, convex, with scattered hairs. Nine pairs of legs. Antennæ 5-jointed, bifid at the extremity, and bearing three, long, jointed appendages.

The author has met with this little Centipede in some numbers, among Thysanura, &c., in his kitchen-garden. He was at first disposed to regard it as a larva; but having, during the last three months, had several hundred specimens under examination without finding any in a more advanced condition, and having found spermatozoa in several, he thought there could be no doubt that it is a mature form.

The body is rather narrower in front. The head consists of two segments; the third segment bears one pair of legs; the fourth, fifth, sixth, and seventh two pairs each. Strictly speaking, however, each of these segments is double. The posterior legs are the longest. Each segment, from the third to the seventh, has on the side a pair of strong bristles. There are also several transverse rows of short club-shaped hairs. The eyes are large and oval. The antennæ are very remarkable, and quite unlike those of any other Myriapods. They are 5-jointed and bifid at the extremity. The first four segments are short. The two branches constituting the fifth are longer and

* Abstract of a paper read before the Linnean Society, Dec. 6, 1866.